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The systematics and evolution of Cambrian graptolites from the Burgess Shale of Canada

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Résumé

Les ptérobranches sont originaires du Cambrien basal (Fortunien) et sont principalement connus pour leurs tubes conservés dans les registre fossile. Les formes les plus anciennes représentent des colonies benthiques arborescences qui ne sont pas largement étudiées en raison de la qualité de la conservation et de l'identification traditionnelle erronée de l'espèce. Pour cette raison, les relations phylogénétiques du groupe ne sont pas clairement connues, principalement des formes les plus basales. Les graptolites des schistes de Burgess (Cambrien moyen) étaient vaguement connus grâce à la présence de *Chaunograptus scandens*, de certaines espèces discutables du genre *Yuknessia* et d'autres matériaux fragmentés non déterminés. Cette étude représente une description complète de *C. scandens*, un consensus pour *Yuknessia simple*x et *Y. stephenensis*, ainsi que le nouveau rapport de *Protohalecium hallianum* et *Mastigograptus sp.* de la localité, également trouvés dans des localités de type Burgess Shale en Utah et en Australie. Les analyses phylogénétiques de 34 caractères morphologiques de ces genres des schistes de Burgess, ainsi que de certains taxons benthiques et planctoniques connus (n = 22), placent ces espèces cambriennes comme formes basales entre le ptérobranche pseudocoloniale *Cephalodiscus* et le graptolite vivant *Rhabdopleura.*

Mots-clés: Hemichordata, Pterobranchia, graptolites, Schistes de Burgess, Paléozoïque, Cambrien, systématique, paléontologie, évolution

Abstract

Pterobranchs originated in the basal Cambrian (Fortunian) and are mostly known by their tubes preserved in the fossil record. The earliest forms represent bushy erect growing colonies that are not widely studied due to preservation quality and species misidentification. For this reason, basal phylogenetic relationships within the group are not clearly established. Middle Cambrian Burgess Shale graptolites were poorly known from the presence of *Chaunograptus scandens*, some debatable species of the genus *Yuknessia*, and other undetermined fragmented material. This study represents a complete description of *C. scandens*, a consensus for *Yuknessia simplex* and *Y. stephenensis,* and the new report of *Protohalecium hallianum* and *Mastigograptus* sp. from the locality, which have also been found in Burgess Shale-type localities in Utah and Australia. Phylogenetic analyses of 34 discrete morphological traits from these Burgess Shale genera and some known benthic and planktic taxa (n=22), place these Cambrian species as basal forms between the pseudocolonial pterobranch *Cephalodiscus* and the living graptolite *Rhabdopleura*.

Key words: Hemichordata, Pterobranchia, graptolites, Burgess Shale, Palaeozoic, Cambrian, systematics, paleontology, evolution

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support. Small carbonaceous fragments of pterobranchs were collected from the Buen Formation, Sirius Passet, Greenland from the Stage 3. Later records consist on more complete species identified up to species level found in different localities. *Sphenoecium wheelerensis* is considered the oldest record of a true colonial graptolite and *Rhabdotubus johanssoni* as the oldest recognized rhabdopleurid.

Figure 2.2. *Chaunograptus scandens* Ruedemann**,** 1931. A) ROM 61106 *C. scandens* in association with an arthropod species; B) ROM 58022 showing the two types of tubes, straight and undulated, from a possible continuous single individual; C) Holotype USNM 83484 showing two individuals in association with a sponge-like species; D) Slab indicating in white triangles several fragments of *C. scandens* with other associated fauna*;* E) BSE image showing the tubes and its alternated autothecal segments.

Figure 2.3. Specimens used for *Yuknessia simplex* description. A) Holotype USNM 35406 is the recognized type for the genus and *Yuknessia simplex,* initially described by Walcott in 1919 from the Trilobite Beds. B) Paratype USNM 35407 reexamination does not show a pterobranch affinity and it may possibly be classified as an algae (LoDuca et al. 2015a); C) Paratype USNM 35408 shows size similarities with *Dalyia racemata* according to Maletz & Steiner (2015), excluding it as a pterobranch form.

Figure 2.4. *Mastigograptus* sp. Ruedemann, 1947. A) ROM 54458 general view; B) ROM 54458 detail of branching theca holding conical appendages, suggesting the presence of a triad budding; C) Three different types of tubes in the colony, all showing fuselli: single narrow, twisted, and single wide conical; D) TMP 2004.11.7 represents a less bushy colony but maintains the similar arrangement as the Miller Pass specimen (showed in A and B); E) BSE image showing regular complete fusellar patterns from the uppermost part of the colony.

Figure 2.5. *Protohalecium hallianum* A) ROM 54480 complete colony; left part represents the upward growing; B) Detail of distal thecae showing a brush-like arrangement and no evidence of branching; C) BSE showing regular fusellar sutures from the single-tubed autotheca; D) BSE showing fusellar sutures and twisted-tubes detail from the central axis in the mid region segment of the colony; E) TMP 2004.11.46 detail of distal thecae comparative to B; F) Basal tubes to be compared with the rightest portion of A.

Figure 2.6. Cladograms showing the phylogenetic relationships within living and fossil pterobranch genera. 1) Strict consensus of 4 equally parsimonious trees from a new technology analysis in TNT including only the same taxa as Mitchell et al. (2013) and no Burgess Shale genera. 2) Strict consensus of 54 equally parsimonious trees from a branch and bound analysis in PAUP considering all taxa. The heuristic analysis produces 52 equally parsimonious trees with a 52% bootstrap value that supports the node of *Dendrograptus* as the sister group of the Graptoloida (*Anisograptus* and *Rhabdinopora*), the remaining branches are supported 100%. 3) Strict consensus of 6 equally parsimonious trees from a new technology analysis in TNT including all taxa. 4) Strict consensus selected from the 6 equally parsimonious trees from the previous analysis that best represents all the relationships from all the trees obtained. Numbers above the nodes and branches represent the synapomorphic characters at that branch followed by the Bremer support values and the relative Bremer support values. Branches were only one value is showed refer to the synapomorphic characters.

Figure 2.7. Strict consensus tree from a heuristic analysis in PAUP of 73 equally parsimonious tree including all 22 taxa showing in each node shows their recognized taxonomic level based on the classification of Maletz, (2014b).

- **TABLES**

List of abbreviations

BSE	Back-scattered electrons
HME	Hirnantian Mass Extinction
PAUP	Phylogenetic Analysis Using Parsimony
ROM	Royal Ontario Museum
SEM	Scanning electron microscopy
TMP	(Royal) Tyrrell Museum of Paleontology
TNT	Tree analysis using New Technology
USNM	United States National Museum (= Smithsonian National Museum of Natural History)

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CHAPTER 1.
An introduction to graptolites

Graptolites are marine colonial pterobranch hemichordates mostly known from their tubes preserved in the fossil record since the early Cambrian. The term often refers to the species grouped in the subclass Graptolithina, which together with Cephalodiscida form the class Pterobranchia (Mitchell et al. 2013; Maletz, 2014b). Considering the genus *Rhabdopleura* as a living graptolite, its zooids are used to reconstruct and infer aspects of the biology of the fossil species. Graptolite colonies consist of soft-bodied zooids connected by stolons, an organic secreted tubarium with fusellar structures observed as full rings or half rings with zigzag sutures along the tube, and a secreted cortex that surrounds it (Maletz, 2017). In general, the zooid body, as in all hemichordates, is comprised of three regions: an oval cephalic shield (prosome); the collar bearing a pair of feeding arms with tentacles (mesosome); and a trunk and contractile stalk (metasome) (Maletz & Cameron, 2016) (**Fig. 1.1**). The presence of a tripartite body shared among pterobranchs and enteropneusts is supported by molecular and cladistic analysis (Mitchell et al. 2013; Maletz, 2019).

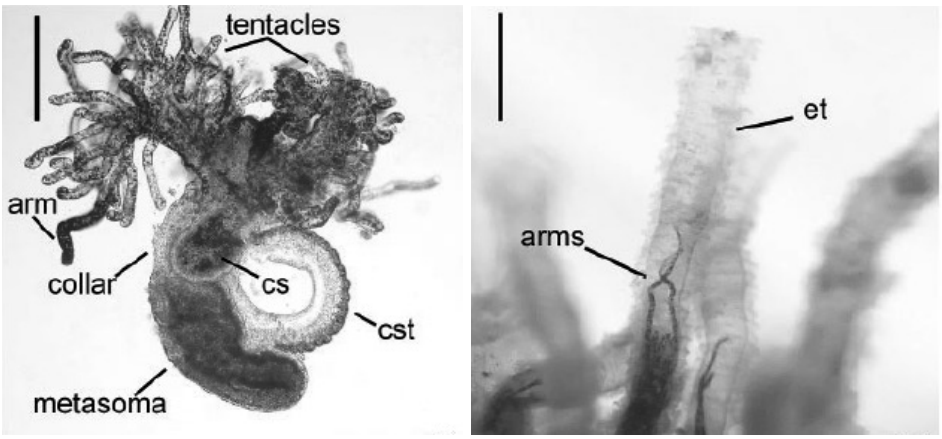

Figure 1.1. Morphology of the living pterobranch *Rhabdopleura recondita.* cs: cephalic shield, cst: contractile stalk, et: erect tube with fuselli. Scale bars: 200 µm (Beli et al. 2018).

Cephalodiscids differ from Graptolithina as they are pseudocolonial organisms, whose zooids hold several pairs of arms, a pair of gill pores, lack specialized thecae (bithecae and autothecae) and have no stolon system so the stalk holding the zooids has an adhesive disc at the base (excepting the genus *Atubaria*) (Bulman, 1970; Maletz & Gonzalez, 2017). Their tubaria can be encrusting and erect, branching and interconnected, similar to graptolites, and their irregularly shaped growth increments are considered homologous to fuselli (González & Cameron, 2012). Graptolithina groups the colonial species that presumably have a pair of arms, lack gill pores, every zooid stalk branches from a common stolon, and the tubes have fuselli (Maletz, 2017). Fossil pterobranchs can be called simply as 'graptolites' when preservation does not allow to observe internal characteristics, hence making their differentiation difficult. It is possible that colonial pterobranchs originated from a non-colonial ancestor like Cephalodiscida, and since non-colonial species also have tubaria, this probably originated before the colonial organization

(Maletz & Steiner, 2015). This view is enforced with the discovery of Cambrian enteropneust fossils that were tubicolous (Caron et al. 2013; Nanglu et al. 2016).

Hemichordate and graptolite tubaria

The presence of housing construction among both hemichordate taxa suggests that this characteristic was present in their common ancestor. The tubarium in pterobranchs comes from the cephalic shield located in the proboscis, which may be supported by the fossil evidence of the proboscis and tube found closely together at one extreme of the tubarium, even though this may be just a preservational feature (Caron et al. 2013). Halanych et al. (2013) discussed the secretion of the tubes from the base of the collar but it comes from an erroneous interpretation of secreted mucuses (Nanglu et al. 2016). A tubarium origin from the glands of the proboscis is more conceivable as it represents a structure known for its mucous secretions important for locomotion and feeding, and in this case, for housing.

The tubes or thecae are part of the tubarium, rhabdosome, or coenoecium which are the main structure found as fossils and forms the compartment where the individual zooids live. The morphology of the tubarium consists of specialized thecae called autotheca and bitheca that create a particular branching pattern. Some species start growing from an encrusting basal part that later forms erect tubes or stipes and whose morphologies can be different, despite being part of the same colony. Depending on the number of thecae at every branching node, graptolite colonies branch divides in diads or triads (Bulman, 1970; Maletz et al. 2016). The former type refers to the presence of two series of autothecae,

while the second type has both autothecae and a new bitheca growing in an alternated pattern (**Fig. 1.2)**.

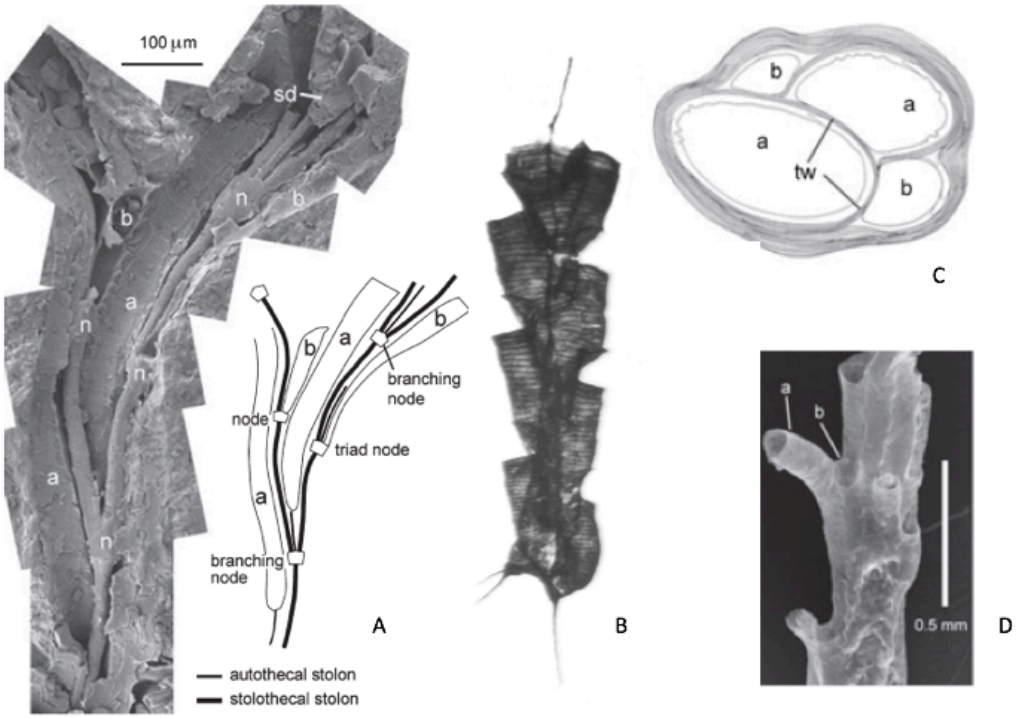

Figure 1.2. Graptolites showing some of their diagnostic characteristics. a: autotheca, b: bitheca, n: node, sd: stolon diaphragm, tw: thecal wall. A) Dendroid colony segment indicating triad thecal differentiation into autothecae and bithecae with its respective stolon material; B) Planktic tubarium with fusellar structures in autotheca; C) Cross-section showing thecal chambers and internal organization of the thecal walls; D) Tubarium with compound stipes that give the twisted appearance observed in some benthic graptolites (Mitchell, et al. 2013).

All graptolites have a main tube, in the oldest literature it is referred as stolotheca since it contains the principal stolon system but it fell into disuse as it represent an immature form of autotheca (Bulman, 1970; Cooper & Fortey, 1983). In dendroid graptolites, branching thecae are associated with the presence of autothecae, which are larger compared to bithecae. This last type is present in some groups, mostly in benthic

species, and is observed as a smaller chamber, either budding at the same origin or showing an alternated pattern with autothecae. Fusellar structures are present in all these types, whether as single full rings or half rings, being the result of a consecutive deposition of granular fabric and fibrils (Maletz et al. 2016). Thecal interconnections between proximate tubes are also observed in some species, creating a complex but organized communication system. Planktic graptolites developed elaborate and diverse thecal structures to support their buoyant lifestyle. All these differences in the tubaria are used as taxonomic traits to differentiate fossil graptolites species.

Although that type of preservation is rare, there are some descriptions of soft tissues preserved, including remnants of zooids and/or stolons with no anatomical detail (Rickards & Stait, 1984; Rickards et al. 1991; Durman & Sennikov, 1993; Loydell et al. 2004; Hou et al. 2011; Hu et al. 2018), however, for some of them, further studies are necessary to support their reliability (Maletz & Steiner, 2015; Maletz & Cameron, 2016). The small size of the zooids and their fast decay in modern pterobranchs suggests that is unlikely to find well-preserved soft tissues in the fossil record (Maletz, 2014a; Beli et al. 2017).

Importance as index fossils and proxies

Studies on the taxonomy of graptolites contribute to the understanding of their diversity and their recognition as individual species who lived in a certain time and space. Graptolites are important index fossils since they have a wide geographic distribution, a great abundance, and evolved an impressive disparity, especially among the graptoloids.

Various species are commonly used in stratigraphy to define biozones and to establish the age of strata, especially in the Ordovician and Silurian periods (Loydell, 2012). Graptolites are also helpful paleoindicators of the conditions in the Paleozoic oceans, for example, in terms of changes in oxygenation (Goldman et al. 2013). A correlation between decreases in their diversity with increases in oxygenation, indicates that they probably had preference for low-oxygen environments or some other parameters of the ocean chemistry sensitive to climate (Maletz, 2017). This idea is supported by the fact that poor oxygen conditions favored the preservation of their organic tubes.

The wide geographical distribution of fossil graptolites includes all marine environments during the Paleozoic, indicating they can be found nearly everywhere (Rickards & Durman, 2006). According to the graptolite paleoprovinces established by Skevington (1973), the latitudinal temperature gradient in the superficial water influenced most of their distribution. Other models explain their distribution considering depth stratification (biozones), water depth, onshore-offshore differentiation, ecological zonation, among others (Goldman et al. 2013). Graptolite fossils are rare, absent or poorly diverse in shallow shelf environments, so they were largely restricted to offshore and deepwater settings, especially in facies of anoxic environments (Maletz, 2017).

Systematics and their problematic affinities

The taxonomic position of pterobranchs has changed over time due to rare and almost lack of preserved soft tissues that represent some of their unique characteristics. The first description of the group was made in 1735 by Linnaeus who coined the genus *Graptolithus*

and referred them as inorganic marks in the rocks (Bulman, 1970). However, it was until Kozlowski (1947) who studied isolated fossils that their pterobranch resemblance was established. He based his ideas on Schepotieff (1905) who recognized the similarity in fusellar structures between fossil graptolites and *Rhabdopleura*. The two authors concepts were not well accepted until years later.

Over time, descriptions placed the group into other phyla and classes including Cephalopoda, Hydrozoa, Polyzoa, and Bryozoa, based on similarities in their colonial lifestyle and general morphology (Bulman, 1970; Rickards & Durman, 2006; Sato et al. 2008, Maletz, 2014a). It is possible that some pterobranchs are still misclassified and referred to other taxa. An example is the genus *Yuknessia* that was initially considered an algae but now is recognized as one of the earliest known pterobranchs from the Cambrian Series 3 after the reexamination of two species where fuselli was identified (Steiner & Maletz, 2012; LoDuca et al. 2015).

Some other species have been restudied (e.g. *Dalyia racemata* and *Malongitubus;* Maletz & Steiner, 2015; Hu et al. 2018) but it is not possible to confirm a pterobranch affinity yet due to poor preservation (LoDuca et al. 2015; Maletz & Beli, 2018). Also the opposite scenario is possible, initially recognized graptolites later reclassified as non-calcified algae (e.g. *Medusaegraptus mirabilis*; LoDuca, 1990). To distinguish graptolites from hydroids or algae, the main difference is the lack of fusellar structures and stolon in those groups (Bulman, 1970).

Actually, Graptolithina is divided in two main orders, Dendroidea and Graptoloidea (Maletz, 2014b) (**Fig. 1.3**). The first group includes the benthic organisms with a bushy

morphology formed by irregular branching, this group includes *Rhabdopleura*, and gave rise to Graptoloidea, the unattached planktic graptolites (Maletz & Cameron, 2016). During this transition to graptoloids in the early Ordovician, some main features changed from dendroids, such as the loss of bithecae, the reduction of the periderm thickness and the number of stipes, which developed a tendency to a scandent position (Rickards, 2005). Planktic graptolites developed a wide diversity of tubarium shapes compared to benthic species due to the constraint of their sessile habit.

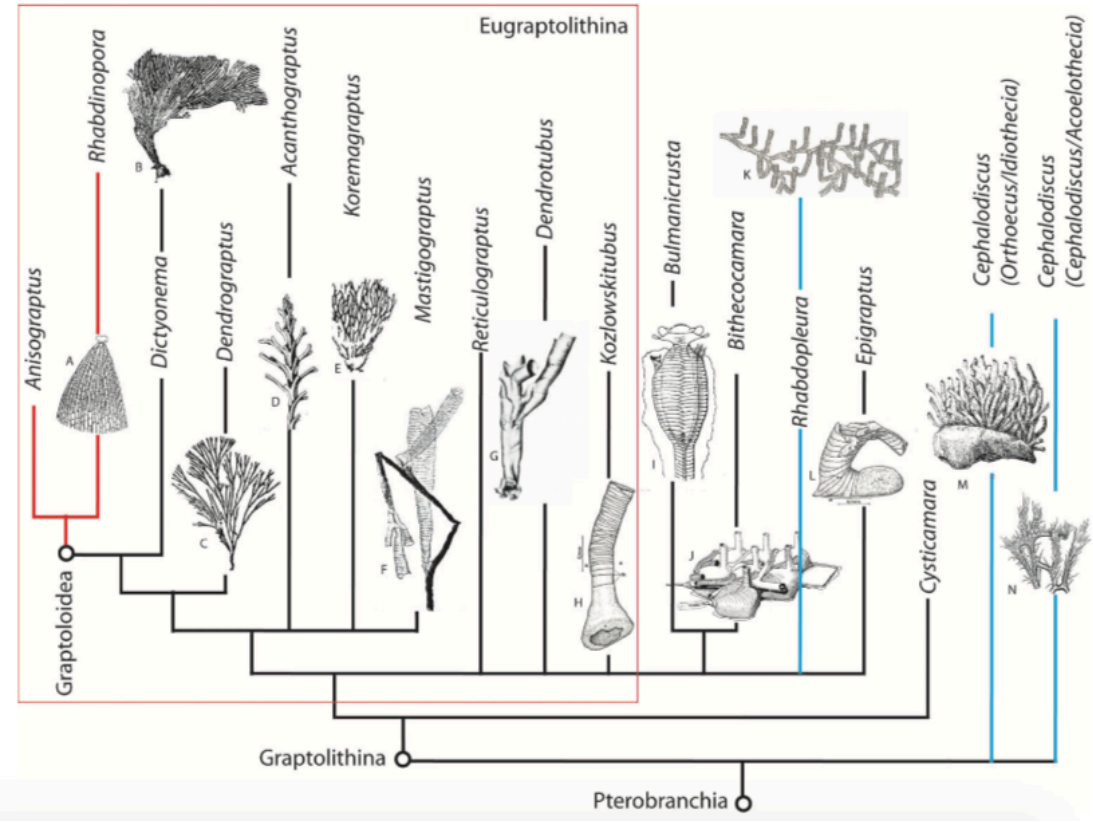

Figure 1.3. Phylogenetic tree of the pterobranchs showing the inclusion of *Rhabdopleura* within Graptolithina and the polytomy indicating the poor resolution of early graptolites. The node Graptoloidea includes the planktic forms and the group Eugraptolithina those who have a prosicula with helical line. In blue are indicated the species that have living representatives (Maletz, 2014b).

The order Dendroidea that persisted from the Middle Cambrian until the Carboniferous (perhaps until the Recent if the living taxa are grouped within), much longer than the Graptoloidea, which appeared in the Lower Ordovician and disappeared in the Lower Devonian (Rickards & Durman, 2006; Maletz, 2014a).

Bias in the study of graptolites

Most studies on graptolites focus on the Ordovician and Silurian fossils because they were abundant and the transition across this chronostratigraphic boundary is characterized by important extinction and radiation events. Before the Hirnantian mass extinction (HME) at the end of the Ordovician, two monophyletic graptoloid lineages diverged in the early Middle Ordovician: the Neograptina and the Diplograptina (Bapst et al. 2012). This second group had more diversity and disparity but nonetheless was driven to extinction during the HME, while the Neograptina rapidly diversified (Chen et al. 2005, Bapst et al. 2012). This replacement of the Diplograptina by Neograptina during the Late Ordovician, placed the group in low paleotropical latitudes, an important biogeographical event for the group (Goldman et al. 2013). After the extinction of the planktic graptolites in the Lower Devonian, the fossil record of graptolites is very poor (Maletz & Cameron, 2016). This detail of information is known for mid-Paleozoic groups, whereas equivalent data on the Cambrian taxa is scarce and consequently the origin and early evolution of graptolites is poorly understood**.**

The graptolite fossil record from the Cambrian is less complete and diverse compared to the Ordovician through Devonian periods (Rickards & Durman, 2006).

Identification of early specimens is difficult due to poor fossil preservation, taphonomic processes, and similarities in morphology between the species. The most common type of preservation in these primitive specimens are films flattened by the weight of the overlying sediment, usually white or silver on a dark background of shale, siltstone or limestone (Rickards, 2005; Maletz, 2014a). The organic material is usually lost by weathering and diagenesis processes and replaced by secondary minerals, or is preserved as dim imprints (Maletz & Steiner, 2014). Under light microscopy, usually only outlines of organic walled fossils are available for determination (Maletz et al. 2005). For all this, SEM studies are needed on Cambrian material to resolve early evolutionary histories (LoDuca et al. 2015).

Rickards & Durman (2006) and Maletz & Steiner (2015) are the main papers where Cambrian graptolites are discussed, providing a general scenario of their early evolutionary relationships but very little is known on their evolution until the origin of planktic graptolites. None of those papers focus on Canada's Burgess Shale graptolite fossils.

Oldest Cambrian graptolite records

Maletz (2019) recognized the oldest pterobranch record from the early Cambrian (Terreneuvian, possibly Fortunian) from fragments identified as *Sokoloviina costata* from the Rovno Horizon, Ukraine (Kirjanov, 1968). Based on this fragments, *S. costata* was later identified in the transition between the Fortunian and Stage 2, from the Lontova Formation in Estonia (Slater et al. 2018). Other small pterobranch fragments have been found in a Burgess Shale-type deposit in North Greenland (Series 2, Stage 3) (Slater et al. 2017), but true colonial pterobranchs (Graptolithina) are known since the early Middle

Cambrian (Series 2, Stage 4) such as *Sphenoecium wheelerensis* (Maletz & Steiner, 2015). Most diverse records are known from the Miaolingian/Series 3 (Steiner & Maletz, 2012; Maletz & Steiner, 2015). The group was considered to be extinct during the Carboniferous until a study by Mitchell et al. (2013) placed the living benthic genus *Rhabdopleura* within the group Graptolithina, as a result of the similarities in the tubarium construction and structure.

Some other early graptolites reported correspond to the basal middle Cambrian of China, in the Burgess Shale-type Kaili Formation where fragments of fusellar wall were collected (Harvey et al. 2012). From the Middle Cambrian of Norway, the single specimen of a benthic graptolite, initially named *Dendrograptus mesocambricus* and *Rhabdotubus johanssoni* from the Middle Cambrian of Sweden were synonymised as *Sphenoecium mesocambricus* by Maletz and Steiner (2015) by similarities in the fusellar structure and branching of the creeping tube (Wolvers & Maletz, 2016).

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CHAPTER 2. Article.

Systematics and evolution of the earliest pterobranchs from the Cambrian Period Burgess Shales of Canada

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INTRODUCTION

Graptolithina is a subclass of cosmopolitan marine colonial pterobranch hemichordates mostly known by their tubes preserved in the fossil record since the Cambrian Period. Graptolites differ from their sister group Cephalodiscida, by the presence of a stolon system that supports a colonial lifestyle, the presence of a larval prosicula, and the morphology of the zooids, that are rarely preserved, yet known from the extant species *Rhabdopleura* (Mitchell et al. 2013; Maletz & Beli, 2018). The subclass comprises the orders Dendroidea, that includes the benthic organisms with an encrusting to erect, bushy morphology formed by irregular branching, as well as the derived Graptoloidea, the unattached planktic forms (Maletz, 2014b; Maletz & Cameron, 2016).

Due to poor fossil preservation, taphonomic processes, and similarities in morphology between taxonomic groups, identification of the specimens is difficult and sometimes mistakenly done, especially in Cambrian forms. The useful criteria to define a graptolite, when the soft-tissue material is not available, include an organic tubarium with

fusellar structures surrounded by secondary cortical tissue, and the stolon system in the Graptolithina (Mitchell et al. 2013). Even when these characteristics are preserved, scanning electron microscopy has to be used to obtain the most details from the specimens; otherwise, mostly outlines of organic-walled fossils are available for determination (Maletz et al. 2005; LoDuca et al. 2015a).

An example of misidentified pterobranchs is the genus *Yuknessia*, which was initially considered as algae (Walcott, 1919) but is now recognized as one of the earliest known pterobranchs from the Cambrian Series 3 due to a SEM re-examination of two species, where fuselli were identified (Steiner & Maletz, 2012; LoDuca et al. 2015a). Like *Yuknessia*, a closer look at other taxa may confirm a potential pterobranch affinity (e.g., *Dalyia racemata* and *Malongitubus;* Maletz & Steiner, 2015; Hu et al. 2018. See Maletz & Beli, 2018 for further discussion). For these early fossils, we refer to them simply as pterobranchs because it is nearly impossible to classify them as cephalodiscids or graptolites.

The pterobranch fossil record from the Early and Middle Cambrian is less complete compared to the Ordovician and Silurian periods (Rickards & Durman, 2006), because of this, the origin and early evolution of graptolites is poorly understood. It is known that early graptolites belonged to the order Dendroidea and persisted from the Early Cambrian until the recent, much longer than the Graptoloidea, which lived from the Lower Ordovician until the Middle Carboniferous (Rickards & Durman, 2006; Maletz, 2014a).

Maletz (2019a) recognized the oldest pterobranch record from the early Cambrian (Terreneuvian, possibly Fortunian) from fragments identified as *Sokoloviina costata* from

the Rovno Horizon, Ukraine (Kirjanov, 1968). Based on these fragments, *S. costata* was later identified in the transition between the Fortunian and Stage 2, from the Lontova Formation in Estonia (Slater et al. 2018). Other small pterobranch fragments have been found in a Burgess Shale-type deposit in North Greenland (Series 2, Stage 3) (Slater et al. 2017), but true colonial pterobranchs (Graptolithina) are known since the early Middle Cambrian (Series 2, Stage 4) such as *Sphenoecium wheelerensis* (Maletz & Steiner, 2015) (See Fig. 2.1). Graptolites were considered to be extinct during the Carboniferous until Mitchell et al. (2013) placed the living benthic *Rhabdopleura* within the Graptolithina, as a result of the similarities in the tubarium construction and structure, demonstrating that at least benthic graptolites survived from the Cambrian to the present.

Acorn worms (Cameron et al. 2000) and pterobranchs (Romer, 1967; Jefferies, 1986) are generally regarded as key groups to understand the origin of the deuterostome phyla (Simakov et al. 2015). However, the Cambrian Period pterobranch fossil record is neither abundant nor well-preserved, so their origin and early evolution is unclear. Rickards & Durman (2006) and Maletz & Steiner (2015) described some Cambrian graptolites and provided a possible scenario of their early evolutionary relationships, neither making a detailed reference to Burgess Shale forms. Herein we provide a taxonomic classification of the pterobranchs from Burgess Shales of British Columbia within the context of other early Paleozoic pterobranch species. We then use these taxa and characters to update the phylogenetic character matrix of Mitchell et al. (2013), in an attempt to resolve the origins and early evolution of the pterobranchs.

METHODS

All the specimens were collected in the Middle Cambrian localities of Walcott Quarry, Miller Pass, Haiduk Peak, and Trilobite Beds, in Southeastern British Columbia, and curated at the Royal Ontario Museum and the Royal Tyrrell Museum. Since the specimens are flat and reflective, they were photographed using direct and cross-polarized light, under dry and wet conditions to capture different details; high resolution photographs were obtained using a Leica M125C stereoscopic microscope.

Backscatter scanning electron microscopy (BSE) was used as a non-destructive technique to reveal ultrastructural characteristics of thin-walled fossils with organic remains, such as the presence of preserved diagnostic fusellar or stolon structures. The fossils analyzed were preserved on sediment surfaces and no isolation attempts were made. Specimens were glued on sample holders and covered with carbon tape to reduce electron charging. All the samples were examined uncoated under low and high vacuum conditions with accelerating voltages of 5-15 kV, at different working distances depending on the thickness of the slabs, on a JEOL JSM-6610LV at the Department of Earth Sciences, University of Toronto. Measurements of the specimens were made through digitally processed images.

SYSTEMATIC PALEONTOLOGY

Hemichordata Bateson, 1885

Class Pterobranchia Lankester, 1877

Subclass Graptolithina Bronn, 1849

Family Rhabdopleuridae Harmer, 1905

Genus *Chaunograptus* Hall, 1882

Type species: *Dendrograptus* (*Chaunograptus*) *novellus* Hall, 1882.

Emended diagnosis: Minute dendroid organic tubarium, creeping and branching, bearing conical unbranched lateral thecae with simple and straight apertures (Bulman, 1970; Maletz & Beli, 2018).

Remarks: The genus was initially considered a hydroid until Obut (1964) classified it as a dithecoid graptolite (Family Chaunograptidae). Mierzejewski (1986) suggested that *Desmohydra* (*D. flexuosa*) and *Epallohydra* (*E. adhaerens*) type species resemble that of *Chaunograptus* and therefore those genera should be treated as synonyms. Maletz (2014b) considered the genus as a hydrozoan based on the idea of Mierzejewski (1986). Maletz & Beli (2018) included *Chaunograptus* in the family Rhabdopleuridae..

Chaunograptus scandens Ruedemann**,** 1931

Figure 2.2

Holotype: USNM 83484 from the Burgess Shale Member, Stephen Formation (Locality 35k Walcott).

Material: ROM 61106, ROM 981517, ROM 58022 from the Walcott Quarry.

Occurrence: Walcott Quarry, Fossil Ridge, Burgess Shale Member, Stephen Formation, Yoho National Park, British Columbia.

Description: Tubarium consists of a slender, straight to undulated stem ranging from 55-135 µm in width, 93 µm average width and up to 150 mm length. Short conical thecae typically 700 µm average length, widening gradually towards the aperture from 90 µm at the base to 135 µm. Thecae develop alternately on the stem, projecting irregularly at

various angles ranging from 80-15°, frequently at angles of 50-60°. Details of the fusellar ultrastructure have not been observed.

Remarks: Slabs contain several short fragments that suggest a continuous arrangement of a single longer colony. It is possible that the smallest tubes are part of the terminal or budding theca supporting the idea of an upward projecting epibenthic suspension feeder. No evidence of branching of the stem was observed. The holotype USNM 83484 also from the Stephen Formation, approaches to the shortest and widest values of the thecal measurements observed from the ROM specimens. One or two fragments of *C. scandens* are present in several slabs from this locality but only those with abundant specimens were used as main material for this description; particularly one slab with both counterparts preserved numerous traces of possibly a single long tube. Tubarium of ROM 61106 resembles that of the holotype by being closely attached to another organism, possibly a sponge but not the same *Tupoia lineata* observed in the holotype (Ruedemann, 1931). ROM 981517 and ROM 58022 specimens contain several *C. scandens* preserved in assemblage with other taxa but not attached to or found near to them. The genus *Chaunograptus* from the Middle Cambrian Burgess Shale may represent one of the oldest colonial pterobranch if fusellar construction can be recognized (Maletz, 2013), however, due to poor preservation, especially by the lack of organic preserved material in the flat specimens and their minute size, only the outline of the colonies has been found preserved. Rickards & Durman (2006) established its taxonomic affinities to the order Dithecoidea based on Obut (1964) but it is no longer a recognized order, after Maletz (2014b) reclassified some of its species into the *incerta sedis* family Dithecodendridae, making no reference to *Chaunograptus*. Maletz & Steiner (2015) assessed that due to the straightness of the tube (that is not always consistent based on the undulated forms preserved) and the short conical thecae, that *C. scandens* may not be related to the known morphology of the type species *Dendrograptus* (*Chaunograptus*) *novellus* but to a possible erect-growing dithecoid. Maletz & Beli (2018) considered the genus to be a member of the Rhabdoleuridae. Backscattered electrons SEM imaging did not show any details of the

fusellar sutures or stolon as organic material traces were not preserved. Most specimens consist of imprints in the sediment and even with SEM only the outline of the tubarium is observed.

Genus *Yuknessia* Walcott, 1919

Figure 2.3

Type species: *Yuknessia simplex* Walcott, 1919 by monotypy.

Emended diagnosis: Isolated long, slender and slightly conical erect tubes non-interconnected, arranged in radiating clusters originated from a circular attachment structure at the base. Rarely branched erect tubes, with evidence of irregular fusellar bands. (LoDuca et al. 2015a & 2015b; Maletz & Steiner, 2015; Maletz & Cameron, 2016).

Remarks: *Yuknessia* was initially classified as a tentative Chlorophyta by Walcott (1919) and future reports of the genus in the USA (Conway-Morris & Robison, 1988; Skinner, 2005) and China (e.g. Hou et al. 1999; Babcock & Zhang, 2001; Guo et al. 2010; Zhao et al. 2011) supported this algal affinity. Maletz & Steiner (2015) found fusellar patterns in a specimen from Utah using backscatter SEM and recognizing its resemblance to *Yuknessia simplex* was classified as a cephalodiscid pterobranch. LoDuca et al. (2015a) redescribed the genus as a 'benthic colonial pterobranch' based on the identification of fusellar bands and other ultrastructural details, and suggested a closely resemblance to rhabdopleurid pterobranchs due to similarities in the suture patterns and budding patterns from the repent tubes, but differing by the distinct zigzag suture and lack of branching in erect tubes in *Rhabdopleura*. Despite these similarities, LoDuca et al. (2015a) did not decide to formally identify the genus as a cephalodiscid or graptolitid, as Maletz & Cameron (2006)

did as well. The presence of a stolon system has not been identified, though this does not necessarily indicate its absence since the lack of a sclerotized sheath that favours its preservation is a possible scenario.

Yuknessia simplex Walcott, 1919

Figures 2.3.A

Holotype: USNM 35406 from the Trilobite Beds, Campsite Cliff Shale Member, Mount Stephen, Burgess Shale Formation, Yoho National Park (Locality 14s Walcott).

Material: ROM 62919, ROM 62920, ROM 62921 from the Trilobite Beds.

Occurrence: Trilobite Beds, Campsite Cliff Shale Member, Mount Stephen, Burgess Shale Formation, Yoho National Park, British Columbia.

Emended diagnosis: Tubarium bears several elongated conical tubes arrayed roughly radially around a black granular object. Slender tubes slightly flexuous ranging from 6-8 mm length, up to 13 mm long, widening distally from 0.1 mm at the base to 0.5 mm towards the aperture. Central (assumed as the repent portion) branching pattern at irregular intervals, bifurcation or interconnections not observed or possibly concealed by the dense overlapped tubes. Fusellar sutures from faint to clearly visible with an average distance of 22 μm. All specimens lack evidence of a stolon system (LoDuca et al. 2015a).

Remarks: *Yuknessia simplex* is the monotypic species of the genus, described by Walcott in 1919 using the holotype USNM 35406 from the Trilobite Beds and two paratypes, USNM 35407 and 35408, from the Phyllopod Bed. The three specimens show notable

morphological differences that indicate two probable species. Maletz & Steiner (2015) considered the holotype as the only specimen that fits in the description of the genus *Yuknessia.* LoDuca et al. (2015a) mentioned that some non-types are consistent with the dimensions of *Dalyia racemata* rather than *Y. simplex,* an idea also supported by Maletz & Steiner (2015); however, a final assignment is limited by the quality of the material and it is conceivable, together with both paratypes, that they are not true pterobranchs. With the reexamination of the types made by LoDuca et al. (2015a), *Yuknessia simplex* is only known from the holotype and other fragmentary specimens from Mount Stephen and no definitive specimens are known from the Walcott Quarry, therefore it should be considered rare and restricted to a Burgess Shale-type locality. Maletz & Steiner (2015) do not deny a possible cephalodiscid nature until clear interconnections or stolon systems are observed in new collected material.

Y*uknessia stephenensis* LoDuca et al. 2015a

Sphenoecium wheelerensis Maletz & Steiner, 2015

Holotype: ROM 62918 from the Trilobite Beds, Campsite Cliff Shale Member, Mount Stephen, Burgess Shale formation, Yoho National Park (Locality 14s of Walcott)

Material: ROM 62918 from the Trilobite Beds

Occurrence: Trilobite Beds, Campsite Cliff Shale Member, Mount Stephen, Burgess Shale Formation, Yoho National Park, British Columbia.

Diagnosis: Tubarium consists of several elongated conical tubes arrayed in roughly radial fashion and emerging around a central repent area covered by overlapping tubes. Definitive branching not evident but overlaps are present. Erect tubes form slightly flexuous, from 7 to 20 mm in length and widening gradually distally from ~0.1 mm at the base to a

maximum of ~0.8 mm at the straight aperture. Fuselli with strong transverse ridges with an average height of 0.032 mm faintly visible in BSE images. All species lack evidence of a stolon system (LoDuca et al. 2015a).

Remarks: *Y. stephenensis* was a new true pterobranch species proposed by LoDuca et al. (2015a) to accommodate the specimens from the Trilobite Beds and all the material from the Spence and Wheeler formations of Utah (Conway-Morris & Robison, 1988), previously assigned to *Y. simplex,* based on the width differences of the erect tubes. Maletz & Steiner (2015) referred some pterobranchs from Germany and that same material from Utah to *Sphenoecium wheelerensis* based on differences mostly in size, structure and erect tubes branching (apparently absent in *Yuknessia*). Therefore, they suggest that *Y. stephenensis* should be restricted merely to its type specimen ROM 62918. Maletz & Steiner (2015) mentioned that *Sphenoecium* is typically represented by an encrusting basal region and the erect, slowly widening theca, however, several Middle Cambrian pterobranchs share this same thecal morphology. Since there is a single holotype for *Y. stephenensis* that occurs in British Columbia, *Sphenoecium wheelerensis* is not considered a species from the region, however, it is possible that both species are alike since their differences are based on features that are not clearly distinguished and resolved. Maletz (2019a) recognizes that *Yuknessia* and *Sphenoecium* may be closely related but since the proximal part of the specimens of the former are poorly preserved, it is difficult to prove this. LoDuca et al. (2015a) mentioned that *Y. stephenensis* resembles other Cambrian pterobranch species such as *Rhabdopleura obuti* from Siberia (Durman & Sennikov, 1993), *Rhabdotubus robustus* from the Czech Republic (Maletz et al. 2005), and *Archaeolafoea monegettae* from Utah (LoDuca & Kramer, 2014). Detailed comparisons may invalidate these similarities and provide support for its separation. For example, *A. monegettae* has an elongated growth rather than the radial arrangement characteristic of *Yuknessia* - although two specimens of *Y. simplex* from the Trilobite Beds show an axial elongated growth (LoDuca et al. 2015a). Also, *R. obuti* has a preserved sclerotized stolon sheath and a different branching pattern than *Y. stephenensis*. The single specimen of *Y. stephenensis* from the Burgess Shale has

similar dimensions to *Y. simplex*, but the Utah specimens are notoriously bigger, especially in terms of tube widths. This difference may not be the result of a taxonomical difference but ecological conditions. For example, Spence Shale and Wheeler Shale localities are 300 km apart, and specimens show differences in length.

Order Dendroidea, Nicholson, 1872

Family Mastigograptidae Bates & Urbanek, 2002

Genus *Mastigograptus* Ruedemann, 1908

Type species: *Dendrograptus tenuiramosus* Walcott, 1879

Emended diagnosis: Bushy, dendroid tubarium with slender, dense-walled stipe and thin-walled, distinctly widening thecae arranged in pairs. Fusellar structure with complete fusellar rings and irregular half-rings sutures. Triad budding present and autothecae/ bithecae are not differentiated by size (Bulman, 1970; Maletz, 2014b).

Remarks: Ruedemann (1908) established this genus based on the notable differences between the type species of the genera *Mastigograptus* and *Dendrograptus* (type is *D. hallianus*). Its taxonomic position is not clear. It was initially referred to the family Chaunograptidae by Bulman (1955), and later to the same family, but in the order Dithecoidea by Obut (1964) that included taxa that preceded dendroids. Afterwards, it was treated as a dithecoid with affinities to dendroids and considered a transitional genus between the two (Chapman et al. 1996). Rickards (1993) placed it in the order Dendroidea and then Bates & Urbanek (2002) decided that it did not belong to the dithecoids or dendroids, and separated it into its own family Mastigograptidae and the order Mastigograptida. Maletz (2014b) referred the genus to the order Dendroidea due to the presence of triad budding.

Mastigograptus sp. Ruedemann, 1947

Figure 2.4

Holotype: USNM PAL249129 from the Lyell Formation, Glacier Lake Canyon, Lake Louise, Alberta.

Material: ROM 54458 and several smaller fragments from the ROM collection from Miller Pass and TMP 2004.11.7 from Haiduk Peak.

Occurrence: Miller Pass, Mount Assiniboine Provincial Forrest, Stephen Formation, Burgess Shale Member and Haiduk Peak, Kootenay National Park, Duchesnay Unit, British Columbia, Canada.

Diagnosis: Colony about 7 cm long by 8 cm wide branching into slender stems bearing short conical autothecae with an average width of 215 µm at the base and lightly increasing to a maximum average of 340 µm width. Autothecae are variable in length from 1.5 to 3.5 mm. Tube width variates between 150-200 µm and their arrangements are different depending on the position on the stipes. Upper tubes are the finest and consist of single tubes. Downwards, tubes become somewhat wider by the interconnection of older thecal compartments. Branching is observed as unilateral to either side but some thecae are found alternated, distance between thecae is variable but tends to be smaller in the uppermost part of the colony. Full rings with regular fusellar sutures are separated by a variable distance between 15-20 µm, zigzag sutures are rare. Single stipes are frequently clustered at the tip of the colony and are more abundant at this point compared to lower stipes. Colonies show an arborescent growth and most of the branching occurs at the base.

Remarks: Autothecal lengths are difficult to measure precisely due to overlapping tubes and coverage by the matrix. Autothecae tend to be longer in the distal part of the colony

and slightly shorter at the base. Johnston et al. (2009) reported the presence of TMP 2004.11.7 and two other graptolite fossils from the Haiduk Peak location, and mentioned their affinity to *M. macrotheca* but because of the absence of triad budding and inflated stolothecae - diagnostics characters according to Bates and Urbanek (2002) - the identification was uncertain. However, the presence of three branches with a shared origin observed in the specimen, suggests the existence of this type of budding. An undetermined species of *Mastigograptus* has been reported for the Burgess Shale-type Cambrian localities in Wheeler and Marjum, Utah, where *Yuknessia* species were also found (LoDuca & Kramer, 2014). Maletz (2019a) refers to specimens from the Tyrrell Museum (see Johnston et al. 2009 and Fig 2.5 herein) as possible dithecodendrids, and recognizes certain morphological similarity to an Ordovician *Mastigograptus* mentioned by Andres (1961).

Genus *Protohalecium* Chapman & Thomas, 1936

Type species: *Protohalecium hallianum* Chapman & Thomas, 1936.

Emended diagnosis: Sinuous branching tubarium with terminal conical thecae more dense in the upper part and slightly separated in the lower region. Thecae narrower at their bases and larger towards the aperture (Bulman, 1970; Chapman & Thomas, 1936; Rickards & Durman, 2006).

Remarks: The genus was defined by Chapman & Thomas (1936) from fragmentary specimens collected from Knowsley East, Victoria, Australia. Quilty (1971) reported more complete and slightly bigger specimens from the Que River. Rickards & Durman (2006) examined and photographed the type species and Quilty's material. Bulman (1970) and Maletz (2014) classified the genus as *incertae sedis*.

Protohalecium hallianum

Figure 2.5

Material: ROM 54480 and ROM 54417 from Miller Pass and TMP 2004.11.46 from Haiduk Peak.

Occurrence: Miller Pass, Mount Assiniboine Provincial Forrest, Stephen Formation, Burgess Shale Member and Haiduk Peak, Kootenay National Park, Duchesnay Unit, British Columbia, Canada.

Description: Elongated dendroid tubarium with one or no branching, bearing short conical theca. Colony length of 6.5 and 11 cm and less than 0.85 cm wide. Main axis is straight to sinuous in some sections, showing the appearance of slender tubes inclined to the axis but oriented in rotation, as a coiled stem. Distal stipes tend to show a single tube composition, as well as autothecae all over the colony. The most basal part of the main axis is around 0.4 mm wide lightly decreasing up to 0.15 mm at the upper section, however, this not a strict pattern along the colony. Autothecae are conical, between 150-250 µm wide at the base to 350-450 µm towards the aperture, with some outlier values up to 600 µm. The average thecal length is 3.5 mm, varying between 2.5-4 mm. The colony is characterized by a concentration of autothecae, especially at the upper section; at the lower part of the colony, parallel autothecae are considerably separated from 0.3 to 0.7 mm. Irregular fuselli are observed along the main stipe and autothecae with rare zigzag sutures. Distance between fusellar sutures varies between 18-22 µm. Other ultrastructural features were not identified.

Remarks: ROM 54480 measurements are at the lower end of those for TMP 2004.11.46. Total length differences can be explained by tubarium fragmentation. The two samples come from different localities but common biota has been identified with other known British Columbia Burgess Shale-type deposits such as Haiduk Peak, 50 km southeast Mount Stephen (as in Johnston et al. 2009). The graptolites from the Duchesnay Unit in Miller Pass belong to a younger zone that those from the Walcott Quarry, however, both are similar in terms of stratigraphy (Johnston et al. 2009). The specimens somewhat

resemble the species *Archaeolafoea monegettae* that was reported from the Wheeler Shale by LoDuca and Kramer (2014), similar to *Yuknessia* that has been found in both British Columbia and Utah. The similarities are mainly in the uppermost part of the colony where autothecal branching patterns are comparable. However, this ROM and TMP specimens have a distinctive elongated sinuous growth and similar dimensions as *Protohalecium hallianum* Chapman & Thomas, 1936 from Victoria, Australia. Quilty (1971) showed ink drawings of the specimens that were later photographed and more completely described by Rickards & Durman (2006). The sinuous nature of the main axis and arrangement of the autothecal branches, particularly in the basal section, indicate that the colony may have been arranged helically in life (Rickards & Durman, 2006). This description represents the first identification and description of fusellar patterns in the species, stolon was not observed.

PHYLOGENETIC ANALYSIS

A phylogenetic analysis was performed using a matrix comprised of 22 taxa and 34 discrete morphological traits. The taxa included most of the pterobranch genera examined in Mitchell et al. (2013), plus the taxa reported here from the Burgess Shale (*Yuknessia*, *Chaunograptus*), and the two species of tubicolous Cambrian acorn worms (*Spartobranchus tenuis* and *Oesia disjuncta*) were used as outgroups. The morphological character traits used were those of Mitchell et al. (2013), with some modifications based on the newest literature (Table 2.1) and added character states considering the biology of the hemichordates (ie. tubes in enteropneusts); these changes are indicated in bold in the character matrix (Table 2.2).

Chaunograptus is very likely to be a graptolite yet this has not been confidently demonstrated by the presence of fuselli. It was included in the analysis because the thecal organization is similar to other benthic forms (acute conical alternated thecae). *Cephalodiscus Orthoecus/Idiothecia* and *Cephalodiscus Cephalodiscus/Acoelothecia* were included as ingroups in the analyses, rather than treated as paraphyletic outgroups as done by Mitchell et al. (2013).

The main challenge when trying to find diagnostic characters in pterobranch fossils is the poor preservation of the tubes and the almost total absence of zooids. In most cases, only outlines or dim imprints of the organic tube remain for identification and with this kind of preservation, small differences in tube structures cannot be easily observed. In these cases, we sometimes find additional characters using computed tomography or scanning electron microscopy.

A list of phylogenetically informative external characters and character states including absence/presence or multistate attributes is provided below. The character descriptions were taken from Kozlowski (1949), Bulman (1970), Urbanek & Mierzejewski (1984), Rickards & Durman (2006), Mitchell et al. (2013), Maletz et al. (2014), Maletz et al. (2016) and focus on structures usually observed in dendroid-like graptolites, meaning that planktic forms may not accurately fit into this terminology.

1) Prosicula: Proximal conical part of the sicula (initial zooid constructed tube) where the larva undergoes metamorphosis (0: absent, 1: vesicular (rounded or truncated), 2: tubular, 3: caudal/pointed);
2) Helical line: Spiral outline around the prosicula (do not confuse with regular fuselli) (0: absent, 1: present);

3) Metasicular opening in prosicula: Refers to the pore left by the emergence of the first zooid in the early development of the tube; it is observed between the prosicula and metasicula. If the change is gradual and smooth is considered as 'primary', whereas 'resorption' is observed as an abrupt angular transition formed by resorption by the first thecal zooid (Mitchell et al. 2013) (0: absent, 1: resorption, 2: primary);
4) Metasicular fuselli: Fusellar growth bands observed in the metasicula (distal tubular part of the sicula) (0: absent, 1: irregular, 2: regular zigzag suture);
5) Spiral astogeny: Coiled growth pattern of the first tube around the sicula (0: absent, 1: present);
6) Serial budding: Sequential zooid budding that originates from the serial stolon system and not other structure like the basal disc (0: absent, 1: present);
7) Internal autothecae in prosicula: Autothecae originates within the prosicula and not in distal regions of the sicula (0: absent, 1: present);
8) Stolon type: General form of the stolon (0: absence, 1: tubular, 2: beaded, 3: unsclerotized/not preserved);
9) Stolon position: Location of the stolon within the tube (0: absent, 1: embedded in basal wall, 2: central, 3: embedded in upper wall);
10) Stolon diaphragms: Globular or cup-like expansion in main stolon at nodes where daughter stolons branch (at the base of autotheca/bitheca); also known as vesicular diaphragms (0: absent, 1: present);
11) Budding type: Number of zooids (or its respective branching theca or stolons) budding at each division, it involves the presence of a new autothecae and sometimes bithecae (0: absence, 1: diad, 2: triad);
12) Thecae with stolon system: Refers to the old term 'stolothecae', that was considered a type of tube enclosing stolon, for almost all dendroid-like graptolites, is the main tube of the colony. If the autotheca is recognized as the main and larger type of graptolite thecae (as it is for Graptoloids), under this parameter, the stolotheca is a synonym of autotheca but as in *immature* form (Bulman, 1970). This character is included based on the presence of a pterobranch species (*Cysticamara*) where the stolon is not

surrounded by thecal tubes but extrathecal tissue (Kozlowski, 1949), besides *Cephalodiscus* and acorn worms where there is no stolon system (0: absent, 1: present);

13) Stolon location within thecorhiza: Position of stolon in the thecorhiza (a compact encrusting basal disc, similar to the creeping tubes in other graptolites) (0: stolon absent, 1: encrusting, 2: on top of thecorhiza, 3: diverse locations within thecorhiza, 4: thecorhiza absent);
14) Encrusting: Type of tube growth that is sideways the surface and not upwards (as the erect tubes), this characteristic is inferred from preservation and/or presence of basal membrane; a synonym is creeping or repent: (0: no, 1: yes);
15) Erect series of interconnected thecae: Erect tubes show any type of stipe connection (see Character 18), excluding erect tubes that are single (0: absent, 1: present);
16) Planktic: Colonies that have a free lifestyle, inferred from the presence of encrusting tubes or *in situ* preservation: (0: no, 1: yes);
17) Paired dimorphic theca: Presence of paired autothecae and bithecae clearly differentiated (0: absent, 1: present);
18) Stipe connection: Type of discontinuous lateral interconnection between branches (0: absent, 1: anastomosis (temporary fusion of lateral walls), 2: dissepiments (connection by cortical material), 3: thecal bridges (permanent, suggested after Maletz, 2019b);
19) Upright planar tubarium: Colony has a two-dimensional arrangement, excluding bushy or colonies growing upwards from their encrusting tubes, that suggest a tridimensional form (0: absent, 1: present);
20) Thecal construction: Refers to the arrangement of the tubes as seen in a cross section (0: irregular, 1: tubular with unshared walls, 2: tubular with shared dorsal walls);
21) Vesicular theca: Presence of any vesicular structure along the tube, like a graptoblast (See Character 26) (0: absent, 1: present);
22) Autothecal isolation: Degree of separation of the new autotheca from the main tube. For some dendroid-like pterobranchs, distal conical branching thecae are called metathecal/autothecal tubes, as assumed to be autotheca (0: non-tubular or irregular, 1: complete or partial, 2: not isolated);

23) Branch condition: Type of stipe branching (0: undefined/absent, 1: stipes possess a single thecal series, 2: compound (single stipe with several thecal series growing along));
24) Fusellar sutures on autothecal tubes: Type of fusellar pattern in erect tubes (0: irregular or absent, 1: zigzag);
25) Autothecal coiling: Autotheca show a spiral coiling of the erect thecal tube (0: absent, 1: present);
26) Closed terminal buds: Refers to the presence of a particular enclosing structure where latent budding zooids develop. Graptoblasts are a type of flattened oval resting cyst with fusellar lines located in the stolotheca and usually observed in old Crustoidea and Camaroidea. A similar, yet less specialized enclosing structure has been observed in *Rhabdopleura* and is coded as 'encapsulated' (See Urbanek, 1984) (0: absent, 1: encapsulated, 2: graptoblast);
27) Conotheca: Large conical theca irregularly developed only in some tuboids (0: absent, 1: present);
28) Bithecae: Short type of theca, smaller compared with the autotheca, usually shows an alternated growth side along the stipes, present in triad budding individuals (0: absent, 1: present);
29) Spongy extrathecal mass: Spongy tissue present around some thecal walls, mostly observed in *Cephalodiscus* and some encrusting species (0: absent, 1: present);
30) Endocortex: Structure of the cortex (laminated cortical tissue that forms the periderm) secreted inside the fusellar tissue, produced by multiple secondary depositions of sheets and intersheet material (0: pseudocortex (intersheet material lacking fibrous elements), 1: paracortex (intersheet material as a condensed meshwork of fibrous elements), 2: eucortex (well defined, straight and parallel fibrils)) (Urbanek & Mierzejewski, 1984);
31) Ectocortex: Structure of the cortex secreted outside or above the fusellar tissue (0: absent, 1: pseudocortex, 2: paracortex, 3: eucortex);

32) Vesicular sheet fabric: Material composed of electron dense, homogeneous, or very densely reticulated pellicle delimiting particular fuselli or layers (Urbanek & Towe, 1974) (0: absent, 1: present);
33) Tube fibrils: Fine fibrous elements that constitute the thecal tubes, similar to those observed in *Oesia disjuncta* (Fig. 4F, Nanglu et al. 2016) (0: absent, 1: present);
34) Coloniality: Inferred by the presence of serial branching and the presence of stolons reported in the literature (0: absent, 1: present).

Unknown states were scored as '?' and polymorphic traits as '0/1/2/...'. Missing characters under the parsimony criterion assign to taxa the character state that would be most parsimonious given its placement on the tree. Therefore, only the characters with no missing data will affect the placement of the taxa. For multistate characters, the condition of 'uncertain' was applied, which takes the variable state that minimizes the tree length. Characters were treated as unordered and with equal weight. Analysis were run using PAUP 4.0b10 (Swofford, 2002) under the assumptions of parsimony using the heuristic and branch-and-bound search algorithm by bootstrapping using 10,000 replicates. Statistics reported include tree length, consistency index, and retention index. New Technology Analyses with default parameters were also performed in TNT (Goloboff et al. 2008), and statistics such as tree length and absolute and relative Bremer support values were calculated. Changes of individual characters along branches were tracked using Mesquite 3.51 (Maddison & Maddison, 2018).

DISCUSSION

The old classification of graptolites by Bulman (1970) recognized most benthic forms in the now disused orders Tuboidea, Camaroidea and Crustoidea and most Burgess Shale or early taxa were considered *incertae sedis* (i.e *Protohalecium*, *Mastigograptus*, *Chaunograptus*, *Sphenoecium*). In the revisited classification by Maletz (2014b & 2017), he discontinued those orders but maintained their families as uncertain taxa. This classification only recognizes the two orders Dendroidea and Graptoloidea, the former includes only the true families Dendrograptidae, Acanthograptidae, and Mastigograptidae. It also distinguishes Cephalodiscida as a subclass and Rhabdopleuridae as an *incertae familiae*. Mitchell et al. (2013), Maletz (2014b), and this phylogenetic analysis invalidate Bulman (1970) cladogram that proposed *Cephalodiscus* and *Rhabdopleura* as sister groups, and the Rickards and Durman (2006) tree that grouped fossil graptolites with *Cephalodiscus*.

Mitchell et al. (2013) based their characters list in a similar previous test made by Rickards & Durman (2006) and excluded all genera that were presumably redundant with other species or for which little morphological information was available. They also assumed *Cephalodiscus* as a paraphyletic outgroup after running initial unrooted trees because the tube-building enteropneusts were unknown at that time. Caron et al. (2013) described the tubicolous enteropneust *Spartobranchus tenuis* and suggested that pterobranchs diverged from a tubular enteropneust ancestor during the early Cambrian, and that tubes were secondary lost in derived acorn worms (Nanglu et al. 2016). A second Cambrian Burgess Shale acorn worm, *Oesia disjuncta* lived inside woven fibrous tubes previously known as the alga *Margaretia dorus* (Nanglu et al. 2016). These discoveries

permitted me to conduct analyses with tubicolous acorn worms as a monophyletic outgroup to the graptolites, and with acorn worms plus *Cephalodiscus* as outgroup taxa.

There is no difference in tree shape or statistics with acorn worms versus acorn worms plus *Cephalodiscus* as outgroups because it does not produces a polarization of characters. *Cephalodiscus* is separated from the graptolites due to their pseudocolonial habit that lacks connecting stolons and by the relatively simple ultrastructural details of the tube walls.

The single-zooid tubes of *C.* (*Orthoecus*) and *C.* (*Idiothecia*) are usually regarded as intermediate forms from the communal-zooid tubes of *C.* (*Cephalodiscus*) and *C.* (*Acoelothecia*) (Gonzalez and Cameron, 2012). Evidently, this cannot be tested considering that only two characters differ between them and two other are uncertainties for *Cephalodiscus* and *Acoelothecia,* and most matrix characters are biased to tube morphology whereas in *Cephalodiscus,* the zooid morphology could provide more characters. This explains why that branch is not fully resolved in my phylogenetic tree (Figure 2.6), however, the basal position in the cladogram indicates its differentiation from graptolites.

The position of *Rhabdopleura* is still debatable within the context of the early pterobranchs due to unresolved relationships at the base of the tree. However, this study supports the idea that *Rhabdopleura* shares a more recent common ancestor with fossil graptolites than with the living pterobranch *Cephalodiscus*, and that it represents an extant graptolite within the Graptolithina. Most Burgess Shale genera fall into that basal unsolved node, despite the challenging attempt to identify the most character states from fossil specimens. The living graptolite *Rhabdopleura* appears to occupy an important

transitionary position between the basal group and the derived Eugraptolithina, characterized by a prosicula with a helical line (characters 1 and 2) (Mitchell et al. 2013).

Cysticamara represents a basal taxon in-between *Cephalodiscus* and graptolites in all tree constructions. Historically, it was considered a camaroid because it has diad budding (no bithecae) (characters 11 and 28) and a vesicular thecae (character 21) that it shares with crustoids (Kozlowski, 1949). This unique character is assumed as a unifying element between these three genera (*Bulmanicrusta*, *Bithecocamara* and *Cysticamara*), which supported by the Rickards & Durman (2006) phylogeny. Although, the presence of a spongy extrathecal mass that surrounds the upperly-embedded stolons, meaning that it is not surrounded by a true stolotheca (character 12), is a characteristic only observed in this genus, and representing a possible primitive character state (Kozlowski, 1949). In contrast, *Cysticamara* also shows characteristics typically observed in most derived graptolites like erect autothecal tubes and stolon diaphgrams (character 10). The information about *Cysticamara* is mostly based on Kozlowski (1949) descriptions and since it may represent one of the very earliest graptolite forms, an in-depth reexamination may fill in some missing character states.

Bulmanicrusta and *Bithecocamara* are sister taxa even though they were classically considered crustoids and camaroids, respectively (Bulman, 1970). *Bithecocamara* is coded here with triad budding as it has bithecae, not a typical characteristic for the diad budding of the cysticamarids, yet the presence of bithecae in some species has been noted by Kozlowski (1949). This budding type instead of representing a main difference may be a trait that unites these two taxa, despite the differences in stolon type and position

(characters 8 and 9) or the presence of graptoblast (character 26). The phylogenetic analysis only included one species of each group because information about their representative species is incomplete. Possibly, camaroids and crustoids are a single group that shares a vesicular thecae (character 21) (Maletz, 2014b).

The exclusion of *Epigraptus* and *Dendrotubus,* separately and in combination with *Chaunograptus,* produces poorly resolved trees with lower support values. The reason why Mitchell et al. (2013) excluded these genera from certain analysis was because they show homoplastic traits (e.g. *Epigraptus* has a bithecae not typical for tuboid graptolites) that alter the tree resolution. These characteristics should not be excluded from the analysis even if the expected character state represents an exception or their origin cannot be clearly explained under the traditional classification. For this reason, both genera were included in most trees, except those for sensitivity analyses (Table 2.3). The cladogram obtained from removing the Burgess Shale taxa (Fig. 2.6.1), resolves the poor basal resolution of Mitchell et al. (2013) tree that included *Dendrotubus* and *Epigraptus*, and show *Epigratus* and *Cysticamara* as intermediate forms between *Cephalodiscus* and *Rhabdopleura* plus other fossil graptolites.

Acanthograptus and *Koremagraptus* are grouped by the presence of a compound branch condition (character 23) showing an anastomosed pattern (character 18). A triad of paired dimorphic thecae with shared dorsal walls defines this branch plus the early planktic genera. Maletz (2014b) included these two taxa within the family Acanthograptidae.

Some 50% majority rule consensus trees resolve with at least a 53 bootstrap support value, the relationship of *Dendrograptus* as the sister taxon of the Graptoloidea

(*Rhabdinophora* and *Anisograptus*), and *Dictyonema* relating with all of them. This branching is unresolved in the strict consensus tree which is generated when all taxa are evaluated, otherwise *Dictyonema* is closer to the Graptoloidea in other trees. The genus *Dictyonema* belongs to the family Dendrograptidae and was considered a key to understand the origin of planktic graptolites with the genus *Rhabdinophora*.

Maletz (2019b) reinterpreted *Dictyonema* as a member of the Acanthograptidae. This reexamination from Silurian specimens of the type species revealed that *Dictyonema* has a tubular thecae on compound stipes (character 23) and lacks true dissepiments as stipe connections (character 18), and therefore shows more similarities with the family Acanthograptidae. This is not completely supported by this analysis as the genus remains closer to the planktic forms. Here the addition of *thecal bridges* as a character state for character 18 and the presence of compound stipes in the character matrix, produced a collapsed node with *Dictyonema* and *Dendrograptus* but maintained the same phylogenetic relationship with the planktic taxa.

Changes from a benthic to a planktic lifestyle are mostly related to modifications in the proximal part of the colony, where the initial zooid starts constructing its tube, driven by the loss of the encrusting habit (character 14). It includes the tendency to develop a caudal prosicula (character 1) (instead of the vesicular shape), where the helical line (character 2) becomes more common. Thecae holding stolon start to grow more proximal within the tube (character 7) and central stolon changes from mainly tubular to unsclerotized (character 8), bearing stolon diaphragms (character 10). This contributed to the predominance of a triad budding type with paired dimorphic thecae in the most

derived forms (characters 11 and 17), presenting complex stipe connections (character 15) that maintain autothecal tubes not completely isolated (character 22) .

The cladograms obtained here from different algorithms vary in terms of how specific collapsed groups could be related within the same node. Burgess Shale genera were the most inconsistent because they lack characters, making it problematic to establish a robust phylogeny, though their basal position within the Graptolithina is evident. The selected cladogram from the 6 equally parsimonious trees (Fig. 2.6.4) is congruent regardless of outgroups and is better resolved for the derived graptolites, and is consistent with the PAUP cladogram (Fig. 2.6.2) where some recognized taxonomic levels discussed above can be identified (see Fig. 2.7) according to Maletz (2014b) classification.

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FIGURES

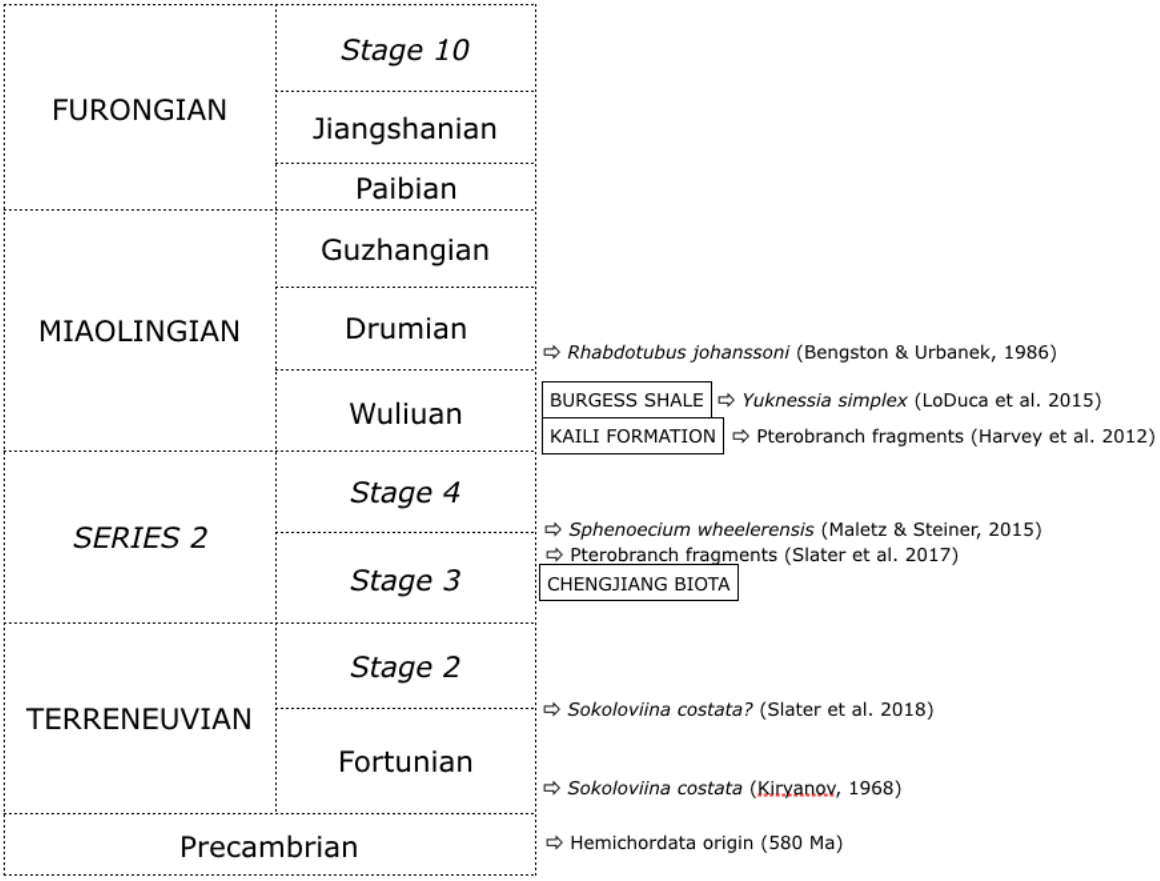

Figure 2.1. Earliest Cambrian pterobranch records, based on organisms that show some features that recognize them as authentic pterobranchs. Molecular clocks estimate the origin of hemichordates in the Ediacaran (580 Ma). Oldest record is *Sokoloviina costata* from the Rovno Horizon, Ukraine (basal Cambrian) and some possible fragments identified as the same species from the Lontova Formation, Estonia from the transition between Fortunian-Stage 2. *Galeaplumosus abilus* was identified as a possible pterobranch zooid from the Chengjiang Biota (Hou et al. 2011), however, a cnidarian affinity has a strongest support. Small carbonaceous fragments of pterobranchs were collected from the Buen Formation, Sirius Passet, Greenland from the Stage 3. Later records consist on more complete species identified up to species level found in different localities. *Sphenoecium wheelerensis* is considered the oldest record of a true colonial graptolite and *Rhabdotubus johanssoni* as the oldest recognized rhabdopleurid.

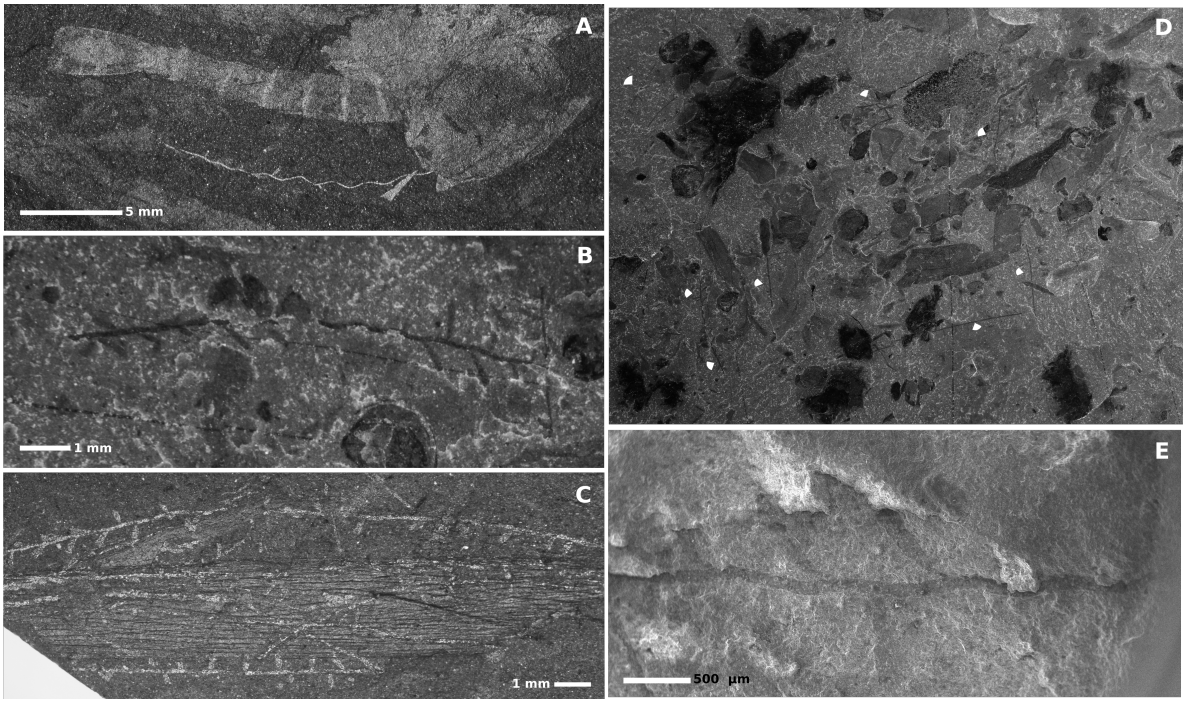

Figure 2.2. *Chaunograptus scandens* Ruedemann**,** 1931. A) ROM 61106 *C. scandens* in association with an arthropod species; B) ROM 58022 showing the two types of tubes, straight and undulated, from a possible continuous single individual; C) Holotype USNM 83484 showing two individuals in association with a sponge-like species; D) Slab indicating in white triangles several fragments of *C. scandens* with other associated fauna*;* E) BSE image showing the tubes and its alternated autothecal segments.

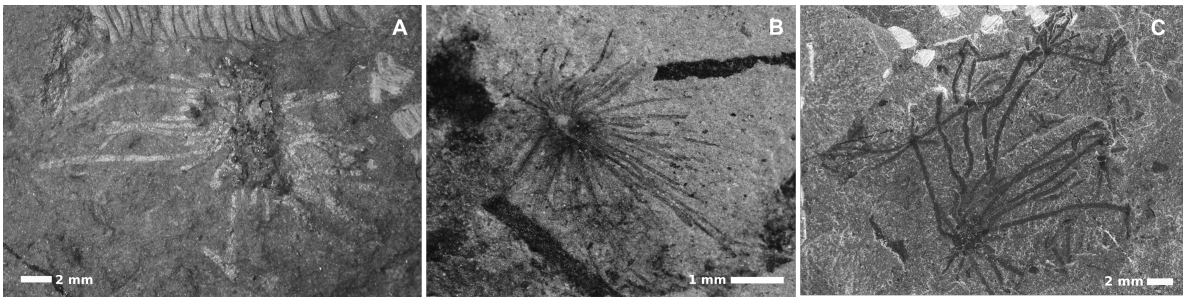

Figure 2.3. Specimens used for *Yuknessia simplex* description. A) Holotype USNM 35406 is the recognized type for the genus and *Yuknessia simplex,* initially described by Walcott in 1919 from the Trilobite Beds. B) Paratype USNM 35407 reexamination does not show a pterobranch affinity and it may possibly be classified as an algae (LoDuca et al. 2015); C) Paratype USNM 35408 shows size similarities with *Dalyia racemata* according to Maletz & Steiner (2015), excluding it as a pterobranch form.

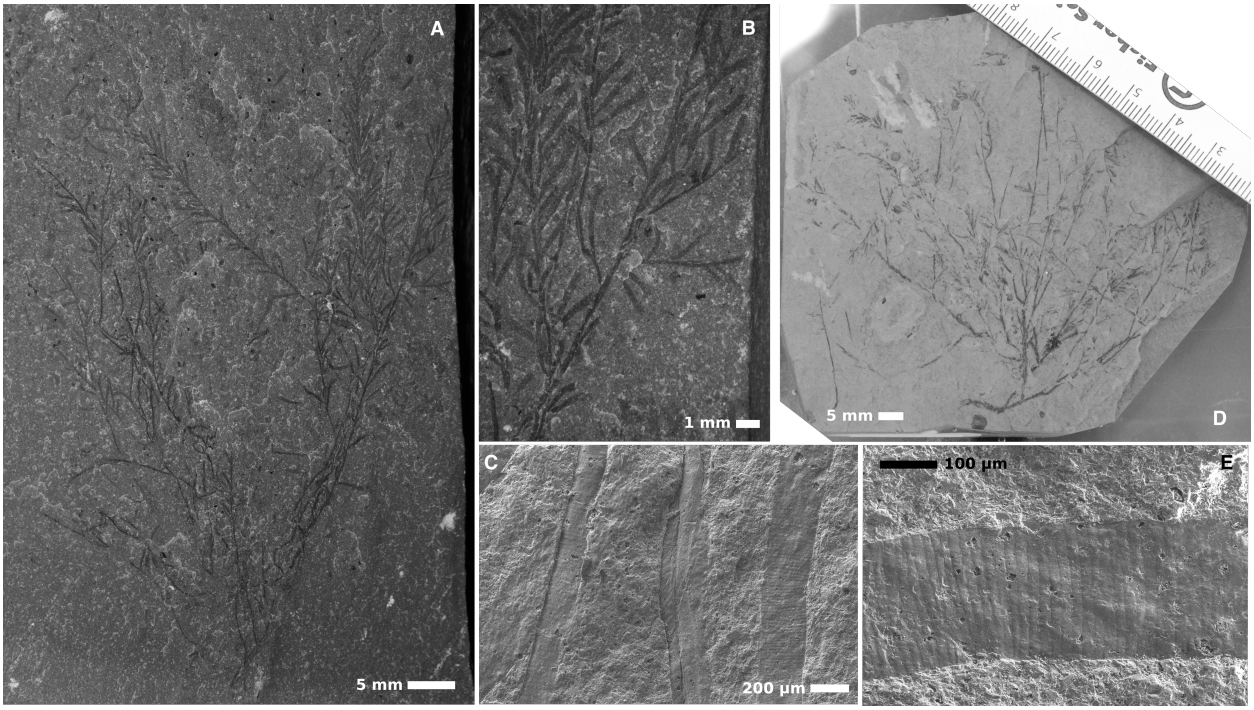

Figure 2.4. *Mastigograptus* sp. Ruedemann, 1947. A) ROM 54458 general view; B) ROM 54458 detail of branching theca holding conical appendages, suggesting the presence of a triad budding; C) Three different types of tubes in the colony, all showing fuselli: single narrow, twisted, and single wide conical; D) TMP 2004.11.7 represents a less bushy colony but maintains the similar arrangement as the Miller Pass specimen (showed in A and B); E) BSE image showing regular complete fusellar patterns from the uppermost part of the colony.

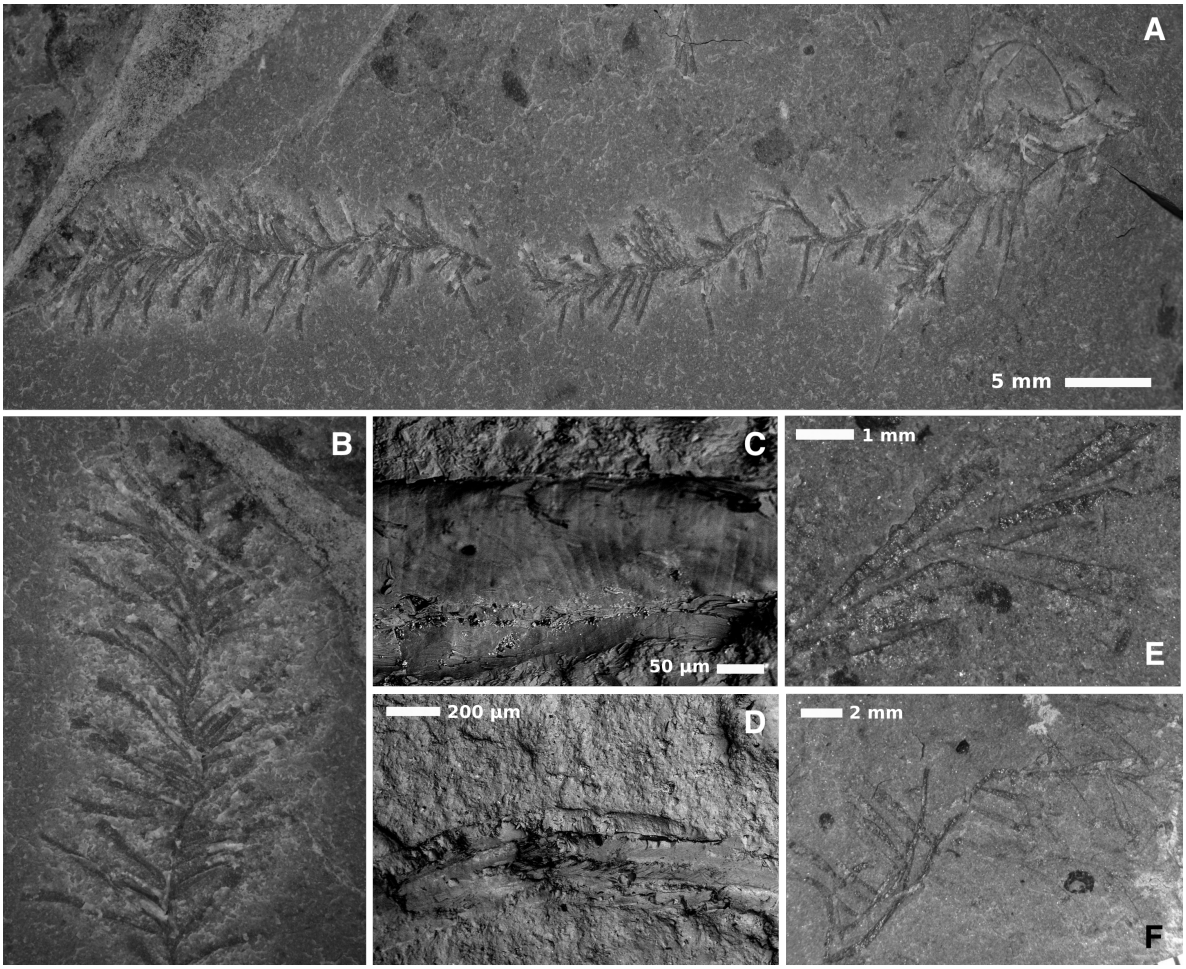

Figure 2.5. *Protohalecium hallianum* A) ROM 54480 complete colony; left part represents the upward growing; B) Detail of distal thecae showing a brush-like arrangement and no evidence of branching; C) BSE showing regular fusellar sutures from the single-tubed autotheca; D) BSE showing fusellar sutures and twisted-tubes detail from the central axis in the mid region segment of the colony; E) TMP 2004.11.46 detail of distal thecae comparative to B; F) Basal tubes to be compared with the rightest portion of A.

Chaunograptus	Ruedemann, 1931; Ruedemann 1947; Urbanek, 1986; Caron & Jackson, 2008; Maletz & Beli, 2018
Yuknessia	Walcott, 1919; LoDuca et al. 2015a; LoDuca et al. 2015b; Maletz & Steiner, 2015
Spartobranchus	Caron et al. 2013
Oesia	Nanglu et al. 2016
Epigraptus	Bengston & Urbanek, 1986; Mitchell et al. 2013
Archaeolafoea	LoDuca & Kramer, 2014
Callograptus	Ruedemann, 1931
Dendrotubus	Maletz et al. 2016
Kozlowskitubus	Mierzejewski, 1988
Dictyonema	Maletz, 2019b
Bulmanicrusta	Maletz, 2014b
Bithecocamara	Maletz, 2014b
Cephalodiscus	Maletz & Gonzalez, 2017
Rhabdopleura	Kozlowski, 1966

Table 2.1. Updated list of literature consulted for the character matrix coding and discussion additional to the sources cited by Mitchell et al. (2013).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Acanthograptus	2/3	?	2	?	0	1	?	1	2	1	2	1	4	**0**	1	0	1	1	0	2	0	1	2	**?**	0	0	0	1	**1**	2	3	1	0	1
Koremagraptus	?	?	?	?	0	1	?	1	2	?	2	1	4	**0**	1	0	1	1	0	2	0	1	2	**?**	0	0	0	1	**1**	2	3	?	0	1
Anisograptus	3	1	2	2	0	1	1	3	2	0	2	1	4	**0**	1	1	1	0	1	2	0	2	1	**2**	0	0	0	1	**1**	2	3	1	0	1
Rhabdinopora	3	1	2	2	0	1	1	3	2	0	2	1	4	**0**	1	1	1	2	1	2	0	2	1	**2**	0	0	0	1	**1**	2	3	1	0	1
Dictyonema	2/3	?	2	?	0	1	1	1	2	1	2	1	4	**0**	1	0	1	**3**	1	2	0	2	**2**	**?**	0	0	0	1	**1**	2	3	1	0	1
Dendrograptus	2	1	2	2	0	1	1	1	2	1	2	1	4	**0**	1	0	1	0	0	2	0	2	1	**2**	0	0	0	1	**1**	2	3	?	0	1
Mastigograptus	2	?	2	?	0	1	?	1	2	1	2	1	4	**0**	1	0	0	0	0	1	0	1	1	**1**	0	0	0	1	**1**	2	3	1	0	1
Reticulograptus	?	?	?	?	?	1	?	1	2	?	1	1	?	**0**	1	0	0	1	1	1	0	1	2	**2**	0	0	1	1	**1**	?	?	?	0	1
Kozlowskitubus	1	1	2	1	1	1	1	1	1/2	1	1	1	1	**1**	1	0	0	2	0	1	0	1	2	**2**	0	0	0	1	**1**	2	3	0	0	1
Dendrotubus	**1**	**1**	**2**	**1**	1	1	**1**	1	2	**1**	1	1	3	**1**	1	0	0	1	0	1	0	1	2	**2**	1	0	0	1	**0**	?	?	?	0	1
Bulmanicrusta	1	0	2	2	?	1	0	2	1	1	**2**	1	1	**1**	0	0	0	0	0	1	1	1	0	**2**	0	2	0	1	**1**	1/2	2/3	0	0	1
Bithecocamara	?	?	?	?	?	1	?	1	2	1	**2**	1	2	**1**	0	0	0	0	0	1	1	1	0	**2**	0	0	0	1	**1**	?	?	?	0	1
Cysticamara	?	?	?	?	?	1	?	1	3	1	1	0	0	**1**	0	0	0	0	0	1	1	1	0	**2**	0	0	0	0	**0**	?	?	?	0	1
Epigraptus	1	0	1	2	1	1	0	1	2	?	**2**	1	3	**1**	0	0	0	0	0	1	0	1	0	**2**	0	0	1	1	**0**	?	?	0	0	1
Rhabdopleura	1	0	1	2	1	1	0	1	2	1	1	1	1	**1**	0	0	0	0	0	1	0	1	0	**1**	0	1	0	0	**1**	2	0	0	0	1
Cephalodiscus CA	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	**0**	?	?	?	0	2
Cephalodiscus OI	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	1	0	1	0	**0**	0	0	0	0	**0**	0	1	0	0	2
Chaunograptus	?	?	?	?	?	1	?	?	?	?	1	1	?	?	0	0	0	0	1	1	0	1	1	?	0	0	0	0	?	?	?	?	0	1
Yuknessia	?	?	1	?	?	1	?	?	?	?	1	1	?	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	?	?	?	?	0	1
Spartobranchus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Oesia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0
Archaeolafoea	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	?	0	0	1	0	1	1	1	0	0	0	?	?	?	?	?	0	1

Table 2.2. Data matrix including 22 pterobranch and enteropneust species of 34 morphological characters used to establish the group relationships. Bold face states are modified from the morphological matrix of Mitchell et al. (2013), plus two additional characters and the Burgess Shale hemichordate species (*Chaunograptus*, *Yuknessia*, *Spartobranchus*, *Oesia*).

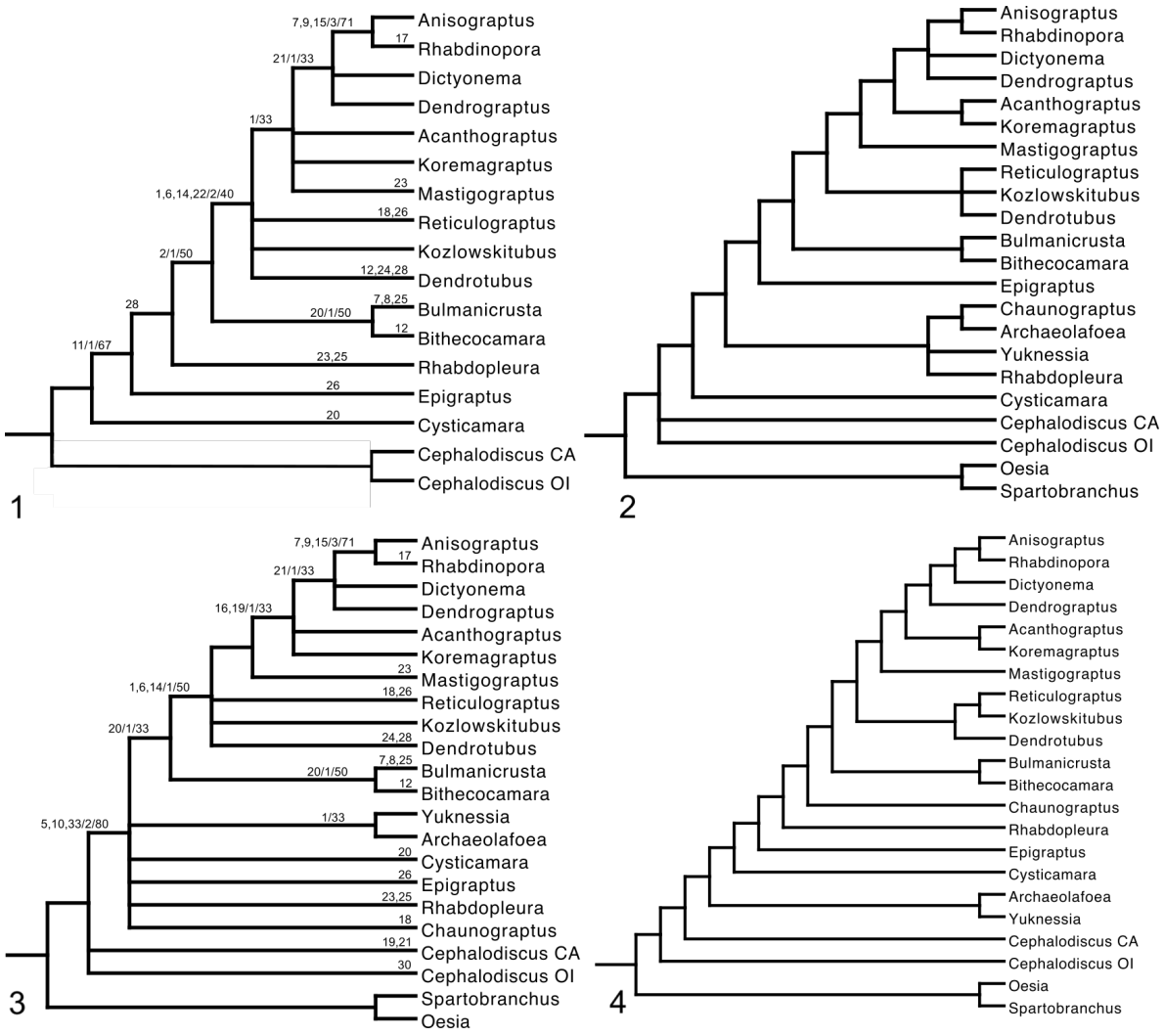

Figure 2.6. Cladograms showing the phylogenetic relationships within living and fossil pterobranch genera. 1) Strict consensus of 4 equally parsimonious trees from a new technology analysis in TNT including only the same taxa as Mitchell et al. (2013) and no Burgess Shale genera. 2) Strict consensus of 54 equally parsimonious trees from a branch and bound analysis in PAUP considering all taxa. The heuristic analysis produces 52 equally parsimonious trees with a 52% bootstrap value that supports the node of *Dendrograptus* as the sister group of the Graptoloida (*Anisograptus* and *Rhabdinopora*), the remaining branches are supported 100%. 3) Strict consensus of 6 equally parsimonious trees from a new technology analysis in TNT including all taxa. 4) Strict consensus selected from the 6 equally parsimonious trees from the previous analysis that best represents all the relationships from all the trees obtained. Numbers above the nodes and branches represent the synapomorphic characters at that branch followed by the Bremer support values and the relative Bremer support values. Branches were only one value is showed refer to the synapomorphic characters.

	All taxa; enteropneusts as outgroup	All taxa; enteropneust + *Cephalodiscus* as outgroup	*Chaunograptus* excluded	*Chaunograptus* + *Dendrotubus* excluded	*Chaunograptus* + *Epigraptus* + *Epigraptus* excluded	*Dendrotubus* + *Epigraptus* excluded	*Chaunograptus* + *Epigraptus* excluded
Tree length	73	73	72	69	65	66	69
CI	0.753	0.753	0.764	0.783	0.815	0.803	0.797
RI	0.876	0.876	0.879	0.885	0.904	0.899	0.896

Table 2.3. Statistical tree values obtained from different sensitivity analyses conducted excluding certain taxa or outgroup using PAUP (CI: consistency index, RI: retention index)

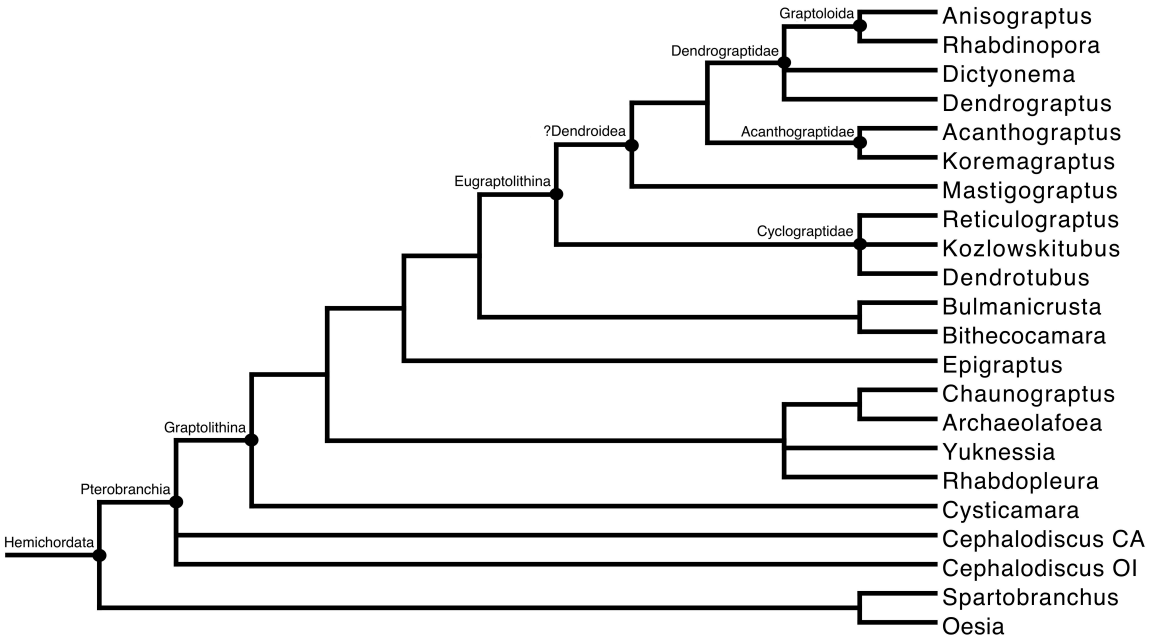

Figure 2.7. Strict consensus tree from a heuristic analysis in PAUP of 73 equally parsimonious tree including all 22 taxa showing in each node shows their recognized taxonomic level based on the classification of Maletz, (2014b).

CHAPTER 3.
Conclusions

This thesis represents the first complete description of graptolites from the Cambrian of Burgess Shale. Several tentatively pterobranch fragments are found in some slabs from British Columbia but the preservation quality and the isolated material represented a challenge for their study. A true pterobranch affinity based on the presence of fuselli was identified for all these specimens (excepting *Chaunograptus*), besides additional morphological characteristics such as tube arrangement and pattern.

The identification of *Mastigograptus* in British Columbia, in addition to other Burgess Shale-type localities from North America are an example of some of the diverse common paleobiota between these early Palaeozoic environments. *Yuknessia* has been reported from British Columbia and Utah, and so are these newly reported graptolite species. In a shorter scale, the presence of a species in two different relatively distant localities (as it is the case of *Mastigograptus* from the Miller Pass and Haiduk Peak) indicate that they had an extensive distribution in the Palaeozoic seas, and the conditions of the environments were alike, as well as the burial deposit.

Thus far *Chaunograptus scandens, Yuknessia simplex,* and *Yuknessia stephenensis* are only known from this locality. However, other *Yuknessia* species from Europe may extend their distribution. *Protohalecium* and *Mastigograptus* have a wider distribution

across North America, Europe and Australia. Due to their presence in the Burgess Shale deposits, the minimum age of these species is from the Middle Cambrian (Stage 3).

The phylogenetic relationship of the group places Burgess Shale species at the base of the cladogram with some intermediate forms between the pseudocolonial *Cephalodiscus* and the living graptolite *Rhabdopleura* and the rest of the colonial species. These basal graptolites represent arborescent benthic and encrusting forms with a relatively simple tubarium characterized by creeping and simple erect tubes showing diverse fusellar patterns. Graptolites later developed more complex and specialized tube patterns in the derived species that favoured their new free lifestyle and allowed a great diversification.

The study of these early forms is greatly limited by the fossils abundance and quality of preservation. Even though Burgess Shale represents a lagerstätte deposit, the pterobranch specimens does not provide more information beyond their general morphology with a glimpse of their internal arrangement. Additional information on their ultrastructure may be obtained from the study with the newest techniques and reexamination of these now described and recognized taxa.